

ON THE SYSTEMATIC POSITION OF ALZATEA VERTICILLATA R. & P.

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In 1953 whilst I was working in Washington my late colleague and friend, Mr. Noel Y. Sandwith of Kew, drew my attention to a specimen of Klug's from Peru, which was very difficult to place in any known family. Sandwith thought it might belong in *Lythraceae*.

To my surprise the same gathering was found in the incertae sedis of most American herbaria and in Stockholm, whilst other specimens of the plant were placed under *Celastraceae*, *Rhamnaceae*, *Guttiferae*, and others.

Independently we identified the plant with *Alzatea verticillata* R. & P. and a collection so named from Bolivia was also found.

However, the systematic position was uncertain and my interest was whetted particularly during a survey of the literature covering the genus *Alzatea*. The problem has hitherto not been solved and this very interesting plant, a tree up to 14 m high from the Amazonian region, still remains without a satisfactory home in any family of the present taxonomic systems.

A historical review of the different attempts at classification is as follows:

Ruiz & Pavón described the genus *Alzatea* in 1794 under *Pentandria Monogynia* and in 1802 the species *A. verticillata*, between *Cervantesia* and *Myoschilos*.

The description of the seeds was drawn up by the authors but remained unpublished until 1954 (*Fl. Per. Chil.* 4, ed. E. A. López). The habitat of the tree, figured in the manuscript of the *Journal* of H. Ruiz, was published in English by Dahlgren in 1946 and by Jaramillo-Arango in Spanish in 1952.

De Candolle in 1824 placed the genus in the *Celastraceae*.

Blume in 1826 when describing *Crypteronia* stated its affinity to be with *Alzatea* "Genus *Alzatea* Ruiz et Pavón valde propinquum."

In 1842 Walpers relegated this genus to *Genera dubia*.

Planchon, 1845, who knew this genus only from the description and plate of Ruiz & Pavón, discussed its affinities and suggested that it should be placed in the *Lythraceae*.

Bentham & Hooker, 1862, following perhaps De Candolle kept the genus within the *Celastraceae*. However, I do not think that this opinion carries any weight since they quoted "ex Ruiz et Pavón" and added "Genus nobis ignotus."

The first detailed description after the original one and its discussion is that of Miers in 1872 where he does agree that the plant is not a member of the *Celastraceae* or of the *Hippocrateaceae* but he suggests that together with *Crypteronia* the two could constitute a tribe (*Crypteronieae*) within the *Rhamnaceae*. This idea was supported especially by the position of the stamens.

In 1911 Hallier reconsidered the question and came to the conclusion that the genus should be placed in the *Lythraceae*. This idea was taken up by Pilger & Kraus (Nachträge, 1915) although Koehne has not followed suit.

Hallier for a second time in 1918, reviewed the problem and suggested the family *Melastomataceae*.

Loesener, the monographer of the *Celastraceae*, quoting Miers, in 1942, eliminated the genus from this family and proposed to include it in the *Rhamnaceae* together with *Crypteronia* and *Tetrataxis* as a tribe of the subgroup *Crypteronieae*.

Subsequently, Macbride (Flora of Peru, 1951) retains *Alzatea* in the *Rhamnaceae* although he suggests affinity with the *Icacinaceae* on some characters and with *Guttiferae* by the leaves.

All these suggestions have tended more towards the rejection of *Alzatea* from the different families than in a search for its proper place. Therefore it was not keyed out in any family and it is not even mentioned in the several editions of the *Syllabus* (1908, 1912, 1924, 1936, 1964)! Its aberrant characters, particularly the parietal placentation have made impossible the naming of any specimen of *A. verticillata*.

DIFFERENCES AND AFFINITIES

1. *Floral and vegetative characters.*

I shall briefly consider the most outstanding differences with the families cited below:

From *Celastraceae*, aestivation, number of ovules, position of the stamens; from *Rhamnaceae*, aestivation, number of ovules (erect), stipules, insertion of petals and stamens; from *Melastomataceae*, leaves alternate, corolla hypogynous, stamens, fruits, etc.; from *Guttiferae*, aestivation, stamens and disk, sepals, etc.

It approaches the *Rhamnaceae* by the aestivation, the parietal placentation and the stamens alternating with the calyx-lobes.

From the *Lythraceae*, the genus *Alzatea* differs only in the placentation (see discussion below). All the other characters are found in the different genera of that family: quadrate section of the branchlets, decussate leaves, inflorescences common to the ligneous genera, consistancy subcoriaceous leaves (*Galpinia*, *Lafoensia*), leaf-venation (*Lafoensia*), perianth 5-6-merous, very frequently found, and its coriaceous consistancy (*Ginoria*, *Galpinia*, etc.), absence of corolla, stamens homomerous, alternate with the calyx-lobes (*Galpinia*, *Tetrataxis*, *Crypteronia*, etc.), anthers with large connective, although they are very peculiar in *Alzatea*, capsular fruit 2-carpelar with two placentae each with two longitudinal series of ovules, dehiscence loculicidal.¹

The placentation of the *Lythraceae* has been recorded as either axillary or central which corresponds in fact to the same type. The ovaries are composed of

¹ The ovary and the fruit have been described as 2-carpelate and 2-locular, but the ovary is in fact 2-carpelate and 1-locular. When the fruit develops, a false septum grows between each pair of placentae towards the centre of the cavity and the capsule thus appears to be 2-locular.

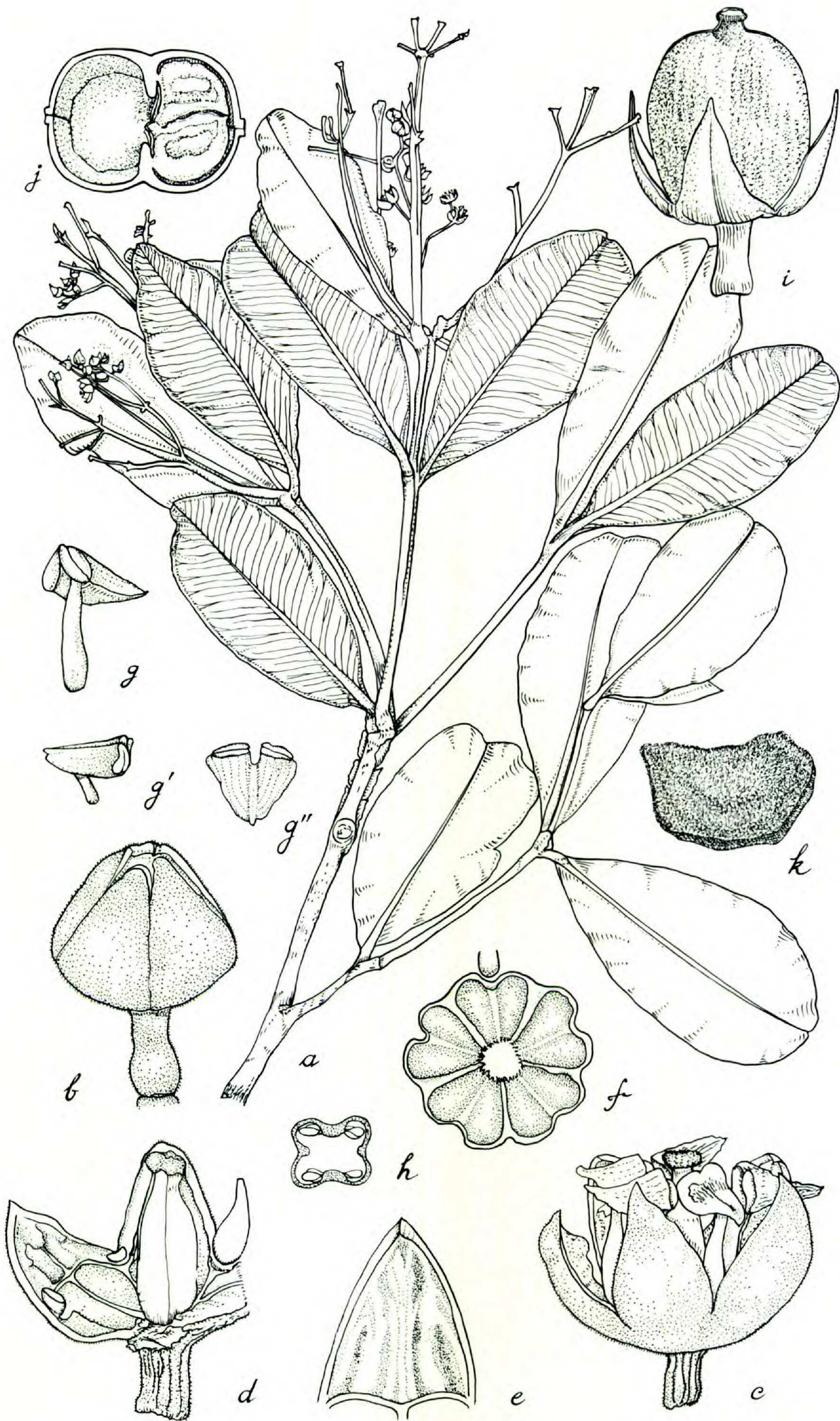


Fig. 1. *Alzatea verticillata*. a, twig $\times 1/2$; b, bud $\times 5$; c, flower $\times 5$; d, part of flower, interior $\times 5$; e, interior of a tepal $\times 7.5$; f, disk $\times 5$; g, g', g'', stamens $\times 5$; h, transversal section of the ovary $\times 7.5$; i, fruit $\times 4$; j, transversal section of the same $\times 4$; k, seed $\times 8$. a-h- from Klug 3349, S; i-k from Woykowski 6196, P. A. Lourteig del.

completely separate locules or the septae are interrupted above the placentae; the number of the ovules is very variable, sometimes very high.

However, the placentation of some genera does not correspond always to the classical definition. The ovary is 1-locular in *Cuphea* with a central free placenta, dorsiventral, with a very characteristic dehiscence. In *Pleurophora* the ovary is 2-locular with a thick central placenta but one of the locules is narrower, sometimes very reduced and sterile (*P. anomala*) and the fruit is not dehiscent. *Diplusodon* shows a 2-locular ovary with a basal placenta bifid and these parts are adnate to the walls of the ovary; they are multiovulate. *Ammannia* subgen. *Cryptotheca* with one species, *A. microcarpa* (a herbaceous plant), occurs in Java, Timor and Celebes, and curiously shows a 1-locular ovary with a parietal placenta (cf. Koehne, Pflreich.).

After all these considerations and a study of Puri's paper, 1952, where he explains the variations and the evolution of the placentation in angiosperms, I have come to the conclusion that the placentation of *Alzatea*, the only character which has prevented botanists from including it in *Lythraceae*, is no bar to such inclusion in view of the other positively "lythraceous characters." To reinforce my conclusions I have had the aid of an anatomist and a palynologist as given below.

2. Anatomical characters.²

a) *Leaf: Lamina.* Dorsiventral. Hairs absent. *Epidermis* with thick cuticle. *Stomata* confined to abaxial surface, ranunculaceous. *Hypodermis* present on either side of the midrib. *Mesophyll* with 2-3 layers of palisade, including large mucilaginous cells. Thick-walled sclereids and large thick walled irregular cells, possibly secretory, frequent in spongy tissue. *Vascular* bundles bicollateral. Midrib with 2 wide, shallow vascular bundles facing each other and 2 small lateral vascular bundles, all with intraxylary phloem, forming an incomplete ring of vascular tissue. Each vascular bundle surrounded by thick-walled fibres. *Crystals* frequent, clustered. Tannin or similar substances frequent in palisade and mesophyll lining abaxial surface. *Petiole.* Elliptical in outline with one face flattened. *Ground tissue.* Outer zone of thick-walled lignified cells. Inner tissue parenchymatous, irregular. Large thick-walled sclereids and secretory sacs frequent. *Vascular bundles.* A large central concentric bicollateral vascular bundle enclosing pith zone. 2-3 small lateral accessory vascular bundles, approximately concentric with intraxylary phloem. *Crystals.* Large clusters very frequent in phloem and also present in ground tissue. (Material from Peru, *Woytkowski 6169*).

b) *Stem: Cork* arising in pericycle; many-layered. *Endodermis* present. Numerous large radially flattened sclereids present in pericycle/secondary phloem. *Phloem* including concentrically arranged crystal cells and sclereids. Phloem and *xylem* in form of continuous cylinder traversed by narrow rays. *Intraxylary phloem* sometimes disintegrated, but evidence of its presence. Pith solid with numerous thick-walled sclerosed cells. *Crystals.* Clusters frequent in phloem. *Wood. Vessels*

² Contributed by Dr. Margaret Y. Stant of the Jodrell Laboratory, Kew Gardens, England.

small, solitary in multiples of 2-3. *Perforations* simple. Intervascular pitting medium, vestured. Pits to rays and parenchyma large and simple. *Parenchyma* scanty. *Rays* uniseriate, occasionally partially biseriate, about 2-12 cells high, heterogeneous. Fibres with simple pits, septate. (Material from Bolivia, *Bang* 890.)

The following characters all of which are mentioned in the description above, appear to indicate that *Alzatea* is closely allied to the *Lythraceae*. Intraxylary phloem, bicollateral vascular bundles. Presence of mucilaginous cells, sclereids and other secretory elements. Pericyclic cork. Vessel pitting. Ray with. Septate fibres. Crystal type and distribution.

3. *Palynological characters*.³

Pollen isopolar, subtriangular, slightly depressed on the axis of the mesocolpium, dimorphic, longiaxial or subaequial in meridional diameter, elliptic to subtriangular. $P = 21-16\mu$, $E = 16\mu$. Pollen tricolporate, ectoaperture elongate narrower towards the equator, endoaperture little visible. Not heterocolporate. Exine finely reticulate not striate, about 1μ . (Material from Peru, *Klug* 3349.)

This pollen recalls that of *Physocalymna* within the *Lythraceae*.

According to Dr. van Campo the pollen resembles that of *Physocalymna* (see Cos-Campos) a monospecific genus; its species (*P. scaberrimum* Pohl) occurs in the Amazonian region and in the Matto Grosso. It is also a big tree but its flowers are very showy with big coloured petals.

CONCLUSION

My research into the affinities of the genus *Alzatea* leads me to believe that the true position of this genus is in the *Lythraceae*. I base this conclusion on the following facts. (1) The floral and vegetative characters are not at variance with those in other genera in the family. (2) The anatomical features of the leaf and stem correspond to similar features found in the *Lythraceae*. (3) The palynological evidence also supports the above views.

Following Koehne's key (Pflreich.) this genus should be placed in the tribe of the *Lythreae* Koehne subtribe II. *Diplusodontinae* Koehne emend. Lourt.:

Subtr. II. *Diplusodontinae*

Semina a dorso compressa circumcirca ala cincta vel spongiosa (quae in *Alzatea*). Fructus maturi placenta maxima depressa, basalis vel placentatione parietali et ovulis 4-serialibus. Flores semper actinomorphi. Aothera dorso affixae.

I. Flores 6-5-meri. Calyx persistens Series I.

γ . Dissepimenta ovarii nulla. In fructo spurium septum inter placentis. Capsula loculicide 2-valvis. Flores homoeomorphi 10a. *Alzatea*.

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Ruiz & Pavón, Prodr. 40, pl. 7. 1784. Hedwig, Gen. 175. 1806. Roemer & Schultes, Syst. 569. 1819. Candolle, Prodr. 2: 10. 1825. Sprengel, Syst. 1: 826. 1825. Blume, Bijdr.

³ Contributed by Dr. Madeleine van Campo of the Palynological laboratory of the Muséum, Paris.

17: 1154. 1826. Reichenbach, *Consp.* 208. 1828; *Handbuch* 301. 1837. Don, *Gen. Syst.* **2**: 11. 1832. Lindley, *Veg. Kingd.* 588. 1833. Spach, *Vég. Phan.* **2**: 404. 1834. Endlicher, *Gen.* 1090. 1836; *Enchir.* 575. 1841. Meissner, *Gen.* 68. 1837. Heynhold, *Nom.* 42. 1841. Planchon, *London J. Bot.* **4**: 476-7. 1845. Bentham & Hooker, *Gen.* **1**(1): 359; 362-3. 1862. Miers, *Tr. Linn. Soc. London* **28**: 328-9. 1872, Pfeiffer, *Nom.* **1**(1): 129. 1873. Engler, *Pflien. Nachtr.* **2-3**: 202. 1908. Hallier, *Med. Rijks. Herb. Leiden* 1910: 29-32. 1911; *Ibid.* **35**: 17-18. 1918; *Ibid.* **41**: 7, nota 2. 1921. Pilger & Krause, *Pflien. Nachtr.* **4**: 188. 1915. Loesener, *Pflien. ed. 1.* **3**(5): 221. 1896; *ed. 2.* **20b**: 196. 1942. Weberbauer, *Pflweit.* **12**: 310. 1911; *Andes per.* 642. 1945. Macbride, *Field Mus. Chicago* **13**(3a, 1): 259, 392-3. 1951. *Alzalia* Dietrich, *Vollst. Lex. Gärtn.* **1**: 299-300. 1802. *Azalea* Walpers, *Rep.* **1**: 539. 1842, ex errore! *Alziniana* Dietr. ex Pfeiffer, *Nom.* **1**: 129. 1873, in synonym!

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Ruiz & Pavón, *Fl. Per. Chil.* **3**: 20, *pl.* 241. 1802; **4**: 123. 1954; *Field Mus. Chicago* **21**: 204. 1940; *Rel. hist.* 322. 1952. Heynhold, *l.c.* 42. Rusby, *Mem. Torr. Bot. Club* **4**: 205. 1875. Macbride, *l. c.* 393.

Alzalia mexicana Dietrich, *l. c.* 299, nomen!

Material seen—PERU. Amazonas, Cerro de Escalero, alt 1300 m, Baum 3-6 m, Bl. gründlichweiss, *Ule* 6750, II 1903, K; Pitabamba, Santa Ana, alt 7-8000 ft, tree 30-40 ft, *Pearce s.n.*, XI 1866, K; San Marín, Zepelacio, nr Moyobamba, alt 1100-1200 m, forest, *Klug* 3349, X-XI 1933, GH, K, MO, S; Río Negro in the forest, alt 1000 m, tree 12 m high, *Woytkowski* 6196, 15 I 1961, MO, P. BOLIVIA. *Bang* 829, K, NY, US.

APPENDIX

I should also recall that *Crypteronia* has all the characters of the *Lythraceae*. The only difference is the polygamous dioecious inflorescence, which has not been found in the family. But I have described a genus for Madagascar, *Capuronia*, a small tree or shrub that is dioecious. Moreover, the anatomy (Metcalf & Clark) is that of the *Lythraceae*. I believe that its right place is that assigned by Bentham & Hooker, that of the *Lythraceae*.

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RÉSUMÉ.

Sur la position systématique de Alzatea verticillata R. & P.—Le genre monospécifique *Alzatea* a été décrit par Ruiz et Pavón parmi le *Pentandria Monogynia*. De Candolle fut le premier à le placer dans une famille. *Celastrineae Tribus II Evonymeae*; il fut suivi par presque tous les botanistes (Reichenbach, Don, Spach, Lindley, etc.), même si dans certains cas le genre était placé parmi les *Genera dubia*, ou genres *incertae sedis*. Sprengel l'a placé dans les *Rhamnaceae*. Blume et Planchon ont trouvé des rapports avec les *Lythracées* et, ce dernier a suggéré de le placer dans cette famille. Mais, les arguments ne furent jamais très convaincants et malgré les diverses tentatives, ce genre s'est vu réjeté des *Celastracées*, *Rhamnaceae*, *Lythracées*, *Hippocrateacées*, *Guttifères*, sans qu'il puisse être classé dans aucune famille.

Il s'agit néanmoins d'un arbre de la forêt amazonienne qui a été récolté plusieurs fois. Bien que la constitution florale et les caractères végétatifs permettaient de placer cette plante parmi les *Lythracées*, la placentation pariétale s'y opposait et ce caractère a constitué la barrière à laquelle les botanistes se sont heurtés.

Heureusement les études modernes sur la placentation et son évolution ont démontré d'une part qu'il n'existe pas une rigidité aussi absolue entre les différents types de placenta-

tion et d'autre part, que, puisque dans l'évolution on peut passer d'un type à l'autre, ce caractère ne doit pas avoir la priorité dans la classification. (Actuellement, plusieurs familles comprennent des genres ayant des types de placentation différents).

Après les observations des caractères systématiques, végétatifs, floraux, de l'anatomie et du pollen, l'auteur arrive à la conclusion qu'il n'y a pas de raison valable qui s'oppose à l'inclusion du genre *Alzatea* dans les *Lythracées*. Il trouverait sa place dans la Tribu des *Lythraeae* Koehne Subtribus *Diplusodontineae* Koehne emend. Lourt.

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